

Clade Perseverance From Mesozoic to Present: a Multidisciplinary Approach to Interpretation of Pattern and Process

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Abstract. Two clades of marine bryozoans, cyclostomes and cheilostomes, exemplify the benefits of applying a multidisciplinary approach to the interpretation of long-term evolutionary patterns. The cyclostome bryozoans were dominant in the Mesozoic; since that era, they have decreased in absolute terms and the cheilostomes have come to exceed them in both abundance and diversity. Many studies of living assemblages of the encrusting members of these two clades indicate that cheilostomes are superior space competitors, but paleontological studies suggest that competition between the two taxa has not been escalating over geological time. Both clades occur throughout the world's oceans and seas, and recent work in the geographical extremes has shown that the relative success of the clades varies markedly from place to place. In this study, the importance of differential patterns of recruitment and cumulative space occupation in the two clades was evaluated over four years and in two environments, one temperate and one polar. In both of these environments, peaks of recruitment and space occupation by the two clades were out of phase. The different strategies and outcomes of spatial competition are examined, largely using data from the literature. Only recently has it been realized that tied outcomes of competition are stable alternative results and not simply transitory phases. Many competitive encounters involving cyclostomes result in ties, implying that their strategy is based on persistence rather than dominance. When different indices and models are used to analyze competition data from the two clades, the interpretation varies markedly with methodology. The differences in patterns of recruitment, space occupation, and spatial competition have influenced

both our understanding of how the two clades have persisted alongside each other and our perception of cheilostome superiority. Analysis of fluid dynamics has shown that small differences in the mechanical structure of typical members of each clade lead to fundamental differences in water movement. For animals that rely on water motion for transport of nutritional and excretory elements (suspension feeders), small changes in current velocity and direction can have a major impact. Preliminary chemical analysis of the excurrent stream leaving cheilostome colonies has shown it to be laden with excretory products, which can interfere and mix with a neighbor's feeding currents. Clearly, spatial competition involves more than a simple mechanical "showdown."

Introduction

During the past two decades, taxon perseverance through geological time has been the center of much paleontological study, which has usually been focused on mass extinctions and radiations. Although the underlying causes of discrete taxon (clade) perseverance may be stochastic, other factors, such as competition, may contribute; but these factors are difficult to assess. Typically, taxonomic richness per unit time has been taken to reflect the scale and pattern of clade survival, whereas the processes involved in clade persistence have been deduced from limited paleontological evidence and inferred from processes that occur in Recent times but are assumed to be equivalent to ones that functioned in the past. However, temporal snapshots of processes such as interference competition can be obtained from the fossilized remains of certain fauna, particularly

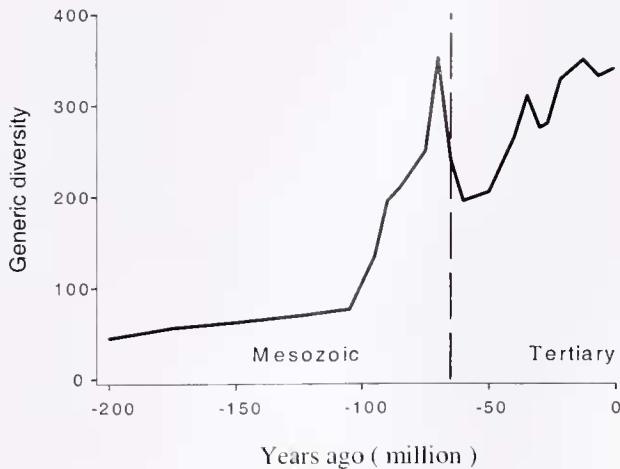


Figure 1. Global generic diversity of cyclostome and cheilostome bryozoans (combined clades) from late Triassic to Holocene times. Data from Taylor (1993) and McKinney *et al.* (1998) based on boundaries designated by Harland *et al.* (1990). The K-T boundary is shown as a vertical dashed line.

those with a high skeletal investment—sedentary lithophyllic encrusters (*e.g.*, bryozoans) foremost among them. Clades that are preserved in this way—that are diverse, abundant, extensive in the fossil record, and extant—offer us the opportunity to apply geological, biological, mathematical, fluid dynamic, and chemical (*i.e.*, multidisciplinary) approaches to understanding the processes underlying persistence.

Cyclostome and cheilostome marine bryozoans, two clades with such attributes, have co-occurred in similar environments for 150 million years. After a long period of

gradual taxonomic increase, they underwent a rapid but punctuated increase in diversity during the Late Cretaceous (Fig. 1). Paleontologists and ecologists have studied these bryozoans extensively, and recent information has clarified the interpretation of scale, pattern, and process in their comparative ecology and evolution. In this manuscript, I examine how two competitor clades have managed to persist alongside one another for more than 100 million years. As background, I first describe the historical patterns of abundance and taxon richness in these bryozoan clades.

Geological Scale and Pattern of Persistence

Cyclostome and cheilostome bryozoans occur together in most benthic lithophyllic assemblages, across latitudinal and longitudinal spectra, and frequently in direct competition for space and food (*e.g.*, Sebens, 1986; Lopez Gappa, 1989; Barnes and Dick, 2000). The older of the two clades, the cyclostomes, are the sole survivors of the class Stenolaemata; they were the dominant bryozoans for 100 million years, throughout most of the Mesozoic (Lidgard *et al.*, 1993) and are still locally important (*e.g.*, Harmelin, 1976). Other clades and paraphyletic or diphyletic groups (see Taylor, 2000) of the class Stenolaemata perished in the mass extinctions that began and ended the Triassic. The explosive radiation of bryozoans 100 million years ago (Fig. 1), comparable in its size to the more familiar success of the euteleost fish and neogastropods (Sepkoski and Hulver, 1985), was largely due to the cheilostome families (Fig. 2). The switch from cyclostomes to cheilostomes, in both species dominance and abundance of individuals, has been drastic, although abundance is slightly decoupled from taxonomic richness (Fig. 3).

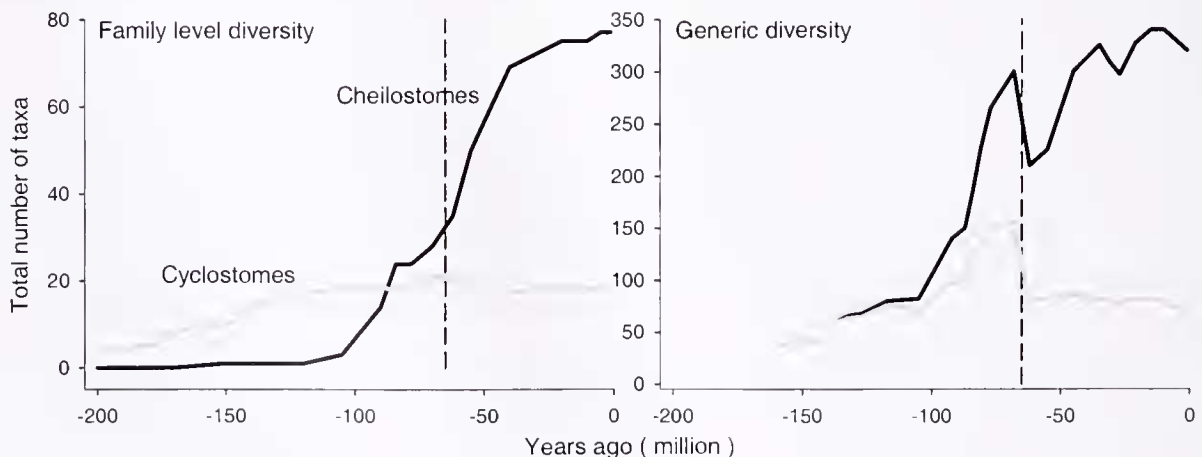


Figure 2. Family- and genus-level diversity of cyclostome and cheilostome bryozoans from Triassic to Recent times. Diversity values are from Taylor (1993) and Sepkoski *et al.* (2000). Family diversity levels (from Jablonski *et al.*, 1997) are absolute for each clade, whereas the generic plot (Sepkoski *et al.*, 2000) shows cyclostomes (lower line) and total (upper line); cheilostome generic diversity is thus equivalent to the divergence of the two lines. The K-T boundary is shown as a vertical dashed line.

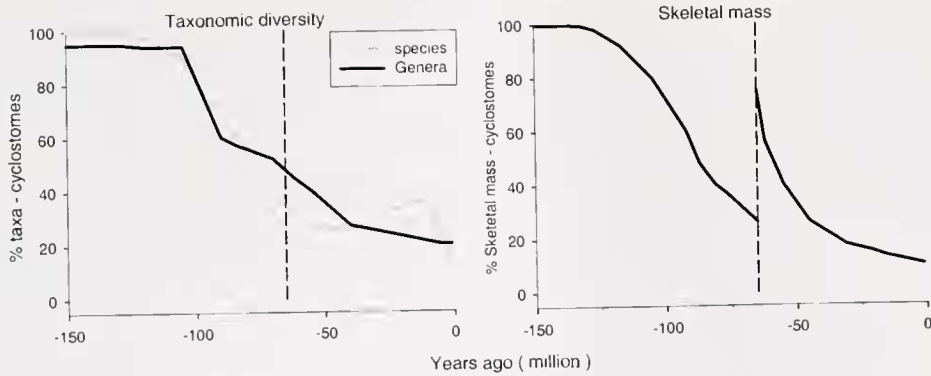


Figure 3. Relative species richness and a measure of abundance (skeletal mass) of cyclostomes and cheilostomes from the Cretaceous to the Cenozoic (from McKinney *et al.*, 1998). Data are trend lines plotted as moving average curves, which are fitted by the distance-weighted least-squares method (see McKinney *et al.*, 1998). The proportion of cyclostomes as a percentage of the total for the two study clades) is shown in the legend. The K-T boundary is shown as a vertical dashed line.

Following the end-Cretaceous mass extinctions, the ecological recovery of cheilostome abundance (measured as % skeletal mass) was slower than that of cyclostomes, taking more than 5 million years, and perhaps 25 million years, to return to Late Cretaceous levels. The competition between the two clades has, however, been stable over the last 100 million years (McKinney, 1995a); that is, cheilostomes have consistently overgrown cyclostomes in two-thirds of their encounters (mean $0.66 \pm \text{SE } 0.11$, $n = 24$, range 0.55–0.75), so this cheilostome superiority has not increased. Cheilostomes in modern assemblages also overgrow cyclostomes, but with significantly more variability than is evident in the fossil record (Barnes and Dick, 2000). Competition is complicated, not only by the conditions of preservation, but also by the ways in which the outcomes are measured (*e.g.*, as a ratio of wins to losses, or wins to total interactions), and by the way that competition data are analyzed (see Petraitis, 1979; Rubin, 1982; Tanaka and Nandakumar, 1994).

Examination of recruitment (*i.e.*, establishment of adult colonies) is another crucial approach to interpreting clade success, as spatial competition occurs only after colonies have formed. This is particularly true with the two bryozoan clades, which generate larvae by different methods and at different times, disparities that might explain the persistence or differential advantages gained by each clade.

In this study, temporal patterns of cyclostome and cheilostome recruitment and persistence were assessed over 4 years and in two very different environments: Lough Hyne (Ireland) and Signy Island (Antarctica). These environments represent extremes in disturbance: the habitat at Lough Hyne has very low energy and relatively warm water, whereas that at Signy Island has cold water that is highly disturbed periodically. The performance of the two clades in overgrowth competition is compared by applying various computations to a model data set (from Barnes and Dick, 2000). I have used both the original data and that from

Barnes and Dick (2000) to address three questions: (1) What characteristics of cyclostomes allow them to persist alongside cheilostomes? (2) What attributes have made cheilostomes superior to cyclostomes in their competition for space? (3) And what are the bases for the proportional and absolute decline of cyclostomes since the K-T boundary?

Materials and Methods

Recruitment and community development at Signy Island, Antarctica

Recruitment of cheilostome and cyclostome bryozoans was measured from 1991 to 1994 at Powell Rock, Signy Island, Antarctica. This is a rocky site that is exposed to ice scour and currents varying from 1 m s^{-1} to $<5 \text{ cm s}^{-1}$. The ecology, composition, and seasonality of the recruit community have been described by Stanwell-Smith and Barnes (1997). The experimental protocol followed that of Todd and Turner (1986). Machined slate panels ($15 \text{ cm} \times 15 \text{ cm} \times 1 \text{ cm}$) were attached, in sets of three, to weighted rods. Two of these triplicate panels were positioned horizontally 1 cm above hard substratum at 25 m depth. Each month, in alternation, one of these two triplicate panels was replaced, and all colonists were counted and identified. Only the central area ($10 \text{ cm} \times 10 \text{ cm}$) of the undersurfaces of the panels was thus analyzed. The mean numbers of cyclostomes and cheilostomes were standardized to recruits per 30-day period, and these values were graphed against time; standard error bars were generated with data from the monthly, three-panel replicates.

Recruitment and community development at Lough Hyne

Recruitment of cheilostome and cyclostome bryozoans was measured from 1997 to 2001 at Lough Hyne Marine Nature Reserve, County Cork, West Ireland. An overview

of the hydrology and marine biology of the site, Labhra Cliff, is given in Kitching (1987). Many environmental parameters at the site are the converse of those at Signy Island. Ambient currents, when measured, did not exceed 5 cm s^{-1} (Maughan, 2000), surface waves were rarely higher than 10 cm, and the maximum water temperature may be more than 20°C (Barnes *et al.*, 2001). Experimental protocol followed Todd and Turner (1986), Stanwell-Smith and Barnes (1997), and that at Lough Hyne (Maughan and Barnes, 2000).

The machined slate panels were set up as at Signy Island, but at two sites, and with two sets of triplicate panels, at 3 m, 6 m, and 12 m depth, at each site. One set of triplicate panels at each site and each depth was replaced (by scuba) each month between October 1997 and May 2001. As with the data generated from the study at Signy Island, the number of recruits from the cyclostome and cheilostome clades was plotted monthly as the mean and standard error. The remaining set of panels was photographed and inspected monthly, and the colonists were identified; the relative amount of space occupied by each clade (% cover) was calculated. After 2 years, these panels were retrieved, analyzed, scraped clean, and repositioned; they were then photographed and inspected monthly for another 18 months. The data on relative space occupation generated from these panels left *in situ* at each depth for 2 years, and then for an additional 18 months, were also graphed.

Interference competition

The outcomes of interference competition between cyclostomes and cheilostomes were recorded on panels at three sites at Lough Hyne and at various depths: Rapids, 3 m; Rapids, 6 m; Whirlpool, 6 m; Whirlpool, 12 m; Labhra, 6 m; and Labhra, 12 m. These study sites constitute an energy gradient with the following, respective, typical current velocities: 3 m s^{-1} , 2.5 m s^{-1} , 1 m s^{-1} , 0.8 m s^{-1} , 0.1 m s^{-1} , and 0.05 m s^{-1} . To boost sample size, cheilostomes were categorized into functional groups (so the interaction outcomes for all species within a functional group were pooled into win, tie, and loss totals), as described in Maughan and Barnes (2000). Functional groups are essentially a set of organisms with similar modes of life and, in the context of interference competition (here), of growth form. The following functional groups were used here: each of the two study clades (cheilostomes and cyclostomes), polychaete worms (phylum Annelida), ascidians (phylum Chordata, subphylum Urochordata), and sponges (phylum Porifera). Outcomes of interference competition were scored as wins, losses, or ties. In accordance with interpretations in the wider literature, a colony that occluded more than 5% of the active zooids of another was awarded a win, whereas its competitor was assigned a loss. Interactions were scored as ties if mutual overgrowth oc-

curred, or if growth was redirected such that a clear "impasse" line was formed. Any tied interaction between representatives of the two clades was monitored further by repeated underwater photographs of interactions, to ascertain the permanency of the outcome.

Treatment of data

Competitive interactions upon the panels at Signy Island and Lough Hyne were used to generate performance scores for site comparisons. These data sets, however, involved too few cheilostome-cyclostome interactions for strong comparisons of different mathematical statistical techniques. Therefore, a data set from the recent literature was selected to illustrate variability in interference competition in a subarctic assemblage (Barnes and Dick, 2000). Competitive "performance scores" of representatives of the two clades were assessed by various methods. The first of these was to calculate, from raw data, the proportion of wins to interactions, and then to rank these values. These "initial rankings" may differ from those of populations because each species participated in a different number of interactions, no species met any of the others on the same number of occasions, and some species never met each other at all. To rectify this problem, the data were standardized; pairwise interactions involving each species were appropriately multiplied such that each totaled 100; total wins, losses, and ties for each competitor identity were then multiplied by the same factor. Several computations were then applied to the standardized values to investigate how the method of assessment would affect the rankings, and thus the apparent success of each species in competition. (1) A scoring system was applied, where a win = 3, a tied outcome = 1, and a loss = 0; wins were rated much higher than ties because ties often prevent further growth and development of colonies; see Barnes and Clarke (1998). (2) The number of wins was divided by the total number of interactions for that competitor. (3) The number of losses was divided by the total number of interactions for that competitor. (4) The number of wins divided by the number of losses for that competitor. (5) In addition, two novel methods from recent literature (see de Vries, 1998; Jameson *et al.*, 1999) were included in this analysis, as they were specifically designed to reduce sources of bias and error in estimating competitor success. These methods are linear ordering procedures based on iterative algorithms (de Vries, 1998) and on mathematical models of paired comparisons involving fairly simple estimations (Jameson *et al.*, 1999); both methods assume that the data form a near-linear hierarchy.

Results

Recruitment at Signy Island, Antarctica

The scale of recruitment of both cheilostome and cyclostome clades was generally comparable throughout the

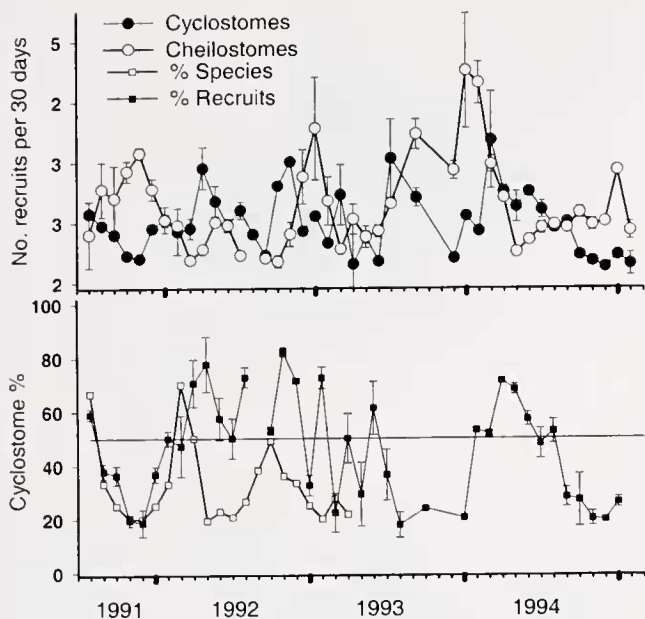


Figure 4. Number and proportion of cyclostome and cheilostome species and recruited colonies, identified at Signy Island, Antarctica, and plotted as a function of time. Data are shown as the mean (from three replicate panels) and standard error. Clade recruitment data were not separated into species after March 1993.

study period (1991–1994) in Antarctic waters (Fig. 4). Monthly, seasonal, and annual variabilities were high in both the timing and magnitude of recruitment in both clades. Between-panel variability was generally low except at peak settlement. But some cheilostome and cyclostome recruits were recorded in every month of the study. Of most note was the aphasic alignment of peak settlement for the two clades. Cheilostomes recruited in peak numbers at the start of the austral summer (December), and cyclostome recruitment usually occurred just before or after peak cheilostome recruitment (*i.e.*, spring and autumn). The proportion of species constituted by cyclostome recruits typically varied between 20% and 40%, but on three occasions was 50% or more. The proportion of recruits that were cyclostomes was, in contrast, considerably higher (especially outside summer periods) and more variable. Only on two occasions was the proportion of recruits smaller than that of the species. Variability in the proportion of recruits was higher than that in the proportion of species, both in space (between panels) and time (between months). Therefore, the phases of recruitment of the two clades were not coincident, but scales were; and abundance of species (taxonomic richness) was decoupled from abundance of individuals (ecological dominance).

Recruitment and community development at Lough Hyne

As at Signy Island, both clades recruited at similar levels during the 4-year study (Fig. 5). Moreover the scale of

recruitment at Lough Hyne was also of a similar magnitude to that at Signy Island, although there were months when there were no recruits of either clade. In contrast to the polar results, most of the variability in recruit numbers was seasonal, but peak recruitment was much greater in 1998 than in any other year in both clades. Between panel variability was very low. Peak recruitment of the two clades was, as at Signy Island, out of phase but in a regular manner: cyclostomes peaked just before cheilostomes in each study year. Peak cheilostome recruit numbers occurred in midsummer (July), and the corresponding cyclostome peak was in May. By species, cyclostomes formed about 20% of recruits in summer but increased to about 70% over each winter. Measured in absolute numbers of recruits, cyclostomes nearly always represented a higher proportion, but this difference varied with season from <30% to >90%. So at Lough Hyne, as at Signy Island, peaks of clade recruitment were similar in scale, but separated in time. The clear distinction between the proportion of recruits and the proportion of their species indicates that, for these two clades, taxonomic richness does not mirror ecological dominance. Patterns in the data collected at 6 m (not shown) were essentially similar to those collected at 12 m (Fig. 5), differing only in the magnitude of the peaks.

Both clades were major components of the cumulative faunal buildup on panels at 6 m and 12 m (Fig. 6), but not on the intertidal panels (not shown). As with the serially replaced panels (Figs. 4 and 5), temporal variability was primarily seasonal, but also annual. Variability changed with depth: seasonal patterns were more distinct at 12 m,

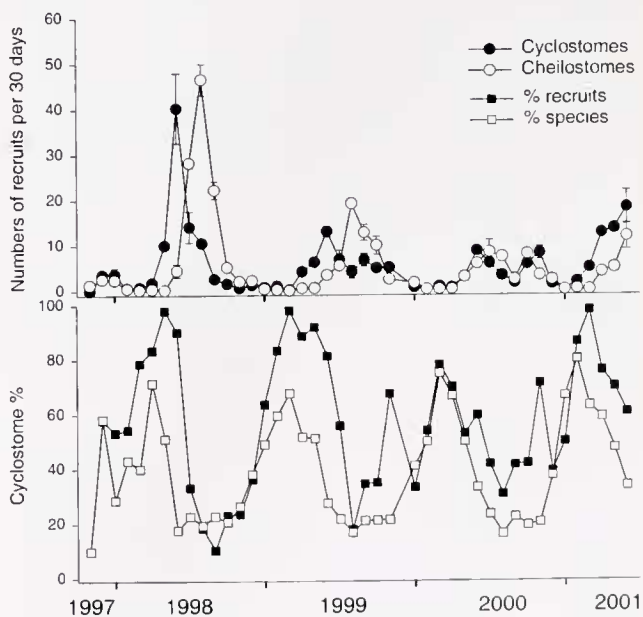


Figure 5. Number and proportion of cyclostome and cheilostome species and recruited colonies collected and identified at Lough Hyne, Ireland, and plotted as a function of time. Data presentation as in Figure 4.

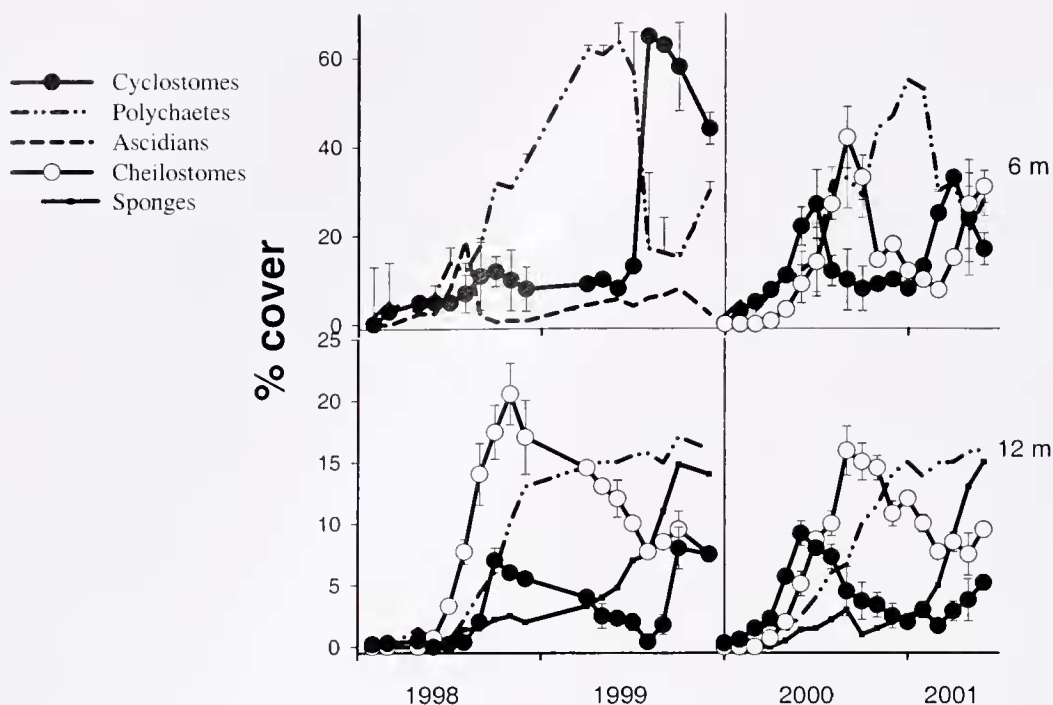


Figure 6. Cumulative space occupation, with time, by marine benthic taxa at Lough Hyne, Ireland. Data are shown as the mean (from three replicate panels) and standard error. The symbols for taxon identity are shown on the figure. Two upper plots represent data from Labhra, 6 m; and the data for Labhra, 12 m, is shown in the two lower plots. Cheilostomes formed a negligible component of the fauna at Labhra, 6 m, in 1998–1999 and are thus not illustrated.

while annual patterns were more distinct at 6 m. The clades peaked at similar year-points at both depths and in the two cumulative runs (1998–1999 and 2000–2001). In contrast to the monthly recruitment patterns, clades differed with respect to scale: cheilostomes typically occupying more space than cyclostomes (despite the similarity in recruitment). At 6 m in 1998–1999, however, the cheilostome buildup was minor despite normal recruitment patterns (pattern as in Fig. 5).

All of the major faunal groups that colonized the panels peaked at different points during the study. Cyclostome space occupation, as with recruitment, peaked both in summer and just before the greatest cheilostome coverage. A clear succession was apparent at 12 m; the cyclostomes were the initial major space occupiers but were replaced sequentially by cheilostomes, polychaetes, and sponges. At 6 m, however, no such succession was apparent in either 1998–1999 or 2000–2001. Faunal groups were sequentially replaced (at 6 m) in 2000 in a pattern similar to that at 12 m, but this pattern appeared to break down in 2001. Curiously, when the experiment was terminated in 1998–1999, cyclostomes were the dominant space occupiers. As for space on the intertidal panels, it was monopolized throughout the study period by barnacles (not shown).

Interference competition and performance assessment

Cyclostomes were poor spatial competitors at Lough Hyne, being overgrown by most other encrusting faunal groups. Against cheilostomes, their performance was average, with a combined win/total interactions score (win index) of 0.44, indicating that cyclostomes win slightly less than half of the encounters. Cyclostome performance varied, however, both with the functional group of cheilostomes with which they competed and with site energy (current velocity) (Fig. 7). With increasing site energy, cyclostomes clearly lost fewer interactions against most of the different functional groups; nevertheless, the improvement in performance increase against some groups was only minor. With a win index of just 0.1, Antarctic cyclostomes at Signy Island were much less effective than those at Lough Hyne at overcoming cheilostomes. When the local performance of cyclostomes (against cheilostomes) was graphed against their local species richness, performance was seen to increase with richness (Fig. 8). Although significant, this correlation must be treated with caution, as it is almost certainly due to the relationship of both parameters with yet other factors.

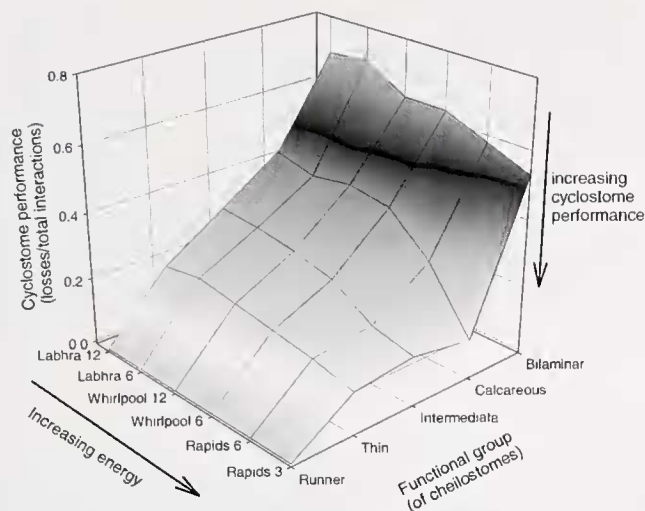


Figure 7. Cyclostome performance in interference competition against functional groups of cheilostomes, plotted as a function of site energy. Performance was measured as proportion of losses in competitive interactions. The cheilostome clade incorporates many colony forms, which are categorized here into the functional groups bilaminar (foliaceous sheets), calcareous (heavily calcified sheets), intermediate, thin (membranous sheets) and runner (stolons). The sites (at Lough Hyne, Ireland) are organized along an energy gradient as shown. For more information on sites, functional groups, or species, see Maughan and Barnes (2000). Performance is measured as L/T , so performance increases as L/T declines.

The highest measured performance of cyclostomes against cheilostomes was in Alaska (data from Barnes and Dick, 2000), but further analysis suggests that the assessment depends on the method of measurement. Initial (non-standardized) and standardized win-tie scored ranking showed cyclostomes to be medium to poor performers against cheilostomes (Table 1). The low proportion of wins to total encounters suggested that *Patinella* (a model cyclostome genus) is a very poor competitor. However, most of the interactions were tied, with the number of wins and losses roughly balancing out. Indeed, the very low proportion of losses was second only to that of the cheilostome *Tegella aquilostris*. Taken together, these observations indicate that although *Patinella* neither won nor lost many encounters, it persisted as a member of the assemblage. This emphasizes that overgrowth performance is not the only mechanism by which a bryozoan can maintain itself in the community. Data were also subjected to two recognized techniques that reduce bias in mathematical comparisons of competitor performance from accumulated pairwise interactions (de Vries, 1998; Jameson *et al.*, 1999). Both measures ranked *Patinella* differently from each other and from previous measures (Table 1), but both suggested approximately medium rankings for the cyclostome genus.

Discussion

What are the implications of differences in recruitment, space occupation, and competition on inter-clade dynamics?

Although the cyclostome and cheilostome clades are similar and occur together on marine hard substrata from the poles to the tropics and from the Mesozoic to present day, their life strategies differ subtly but importantly. Cyclostomes occupy less space and have lower species richness in the temperate and polar study localities, but the intensity of their recruitment is similar to that of cheilostomes (Figs. 4 and 5). More important perhaps, peak levels of recruitment for the two clades are out of phase; cyclostome recruits are typically a month or more ahead of cheilostomes. The reproductive strategy of cyclostomes—which is termed polyembryony and involves repeated cleavage of blastomeres to give large numbers of genetically identical embryos (Harmer, 1893)—may help explain both the high and early recruitment observed in the present study. That peak cyclostome recruitment precedes that of cheilostomes is important for two reasons. First, it maximizes the potential of the clade to occupy temporarily available space. Second, most cyclostomes have grown for a month longer than the same cohort of cheilostomes and thus have the potential advantages of size both in spatial competition and in achieving reproductive activity. The early cyclostome recruitment explains the initial dominance of space by cyclostomes in both Ireland and Antarctica. Six months later, however, cheilostomes occupy more space and are overgrowing cyclostomes. In conclusion, although competitive performance varies with the functional group of cheilostome competitors (Fig. 7), methods of mathematical analysis (Table 1), local cyclostome species richness (Fig. 8), and energy of the environment (in roughly descending order), cheilostomes are overall superior space competitors.

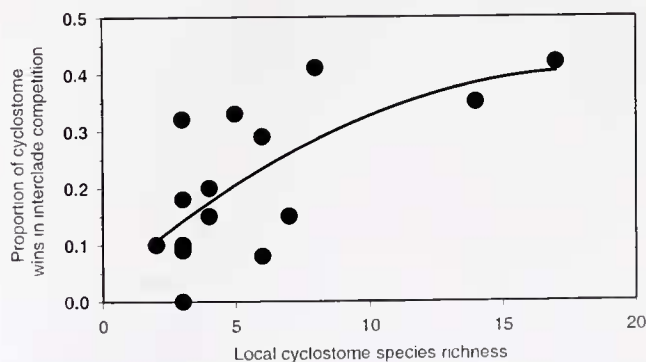


Figure 8. Competitive performance of cyclostomes (against cheilostomes) plotted against local cyclostome species richness. Observations made at Signy Island, Antarctica; data from Barnes and Dick (2000).

Table 1

Alaskan cheilostome and cyclostome bryozoans ranked according to their performance in interference competition

	Initial	Win-Tie score	Win/Total	Loss/Total	Win/Loss	De Vries (1998)	Jameson <i>et al.</i> (1999)
1	Ta	Tq	Tq	Tq	Ta	Ta	Ta
2	Tq	Ta	Ta	P	Tq	Tq	Mp
3	Mp	Mp	Mp	Ta	Mp	Mp	Tq
4	Ca	Ca	Tr	Mp	Ca	Ca	P
5	Mc	Tr	Ca	Ca	P	Tr	Mc
6	Tr	Mc	Mc	A	Tr	A	Tr
7	P	P	M	Tr	Mc	P	Ca
8	M	M	Cn	Mc	A	Mc	A
9	Cn	A	P	Cn	M	Cn=	Cn
10	Pa	Cn	A	Pa	Cn	Pa=	Pa
11	A	Pa	Pa	M	Pa	M=	M

Data from Barnes and Dick (2000) were variously manipulated, and the resulting values are ranked. The rankings, in descending order (1 = best, 11 = worst) can be initial (number of wins/total number of interactions) or standardized (multiplied so every competitor meets the others with the same frequency). The standardized ranking are win-tie scored (wins score 3, ties score 1, so a species with 10 wins, 2 ties, and 88 losses scores $[10 \times 3] + [2 \times 1] + [88 \times 0] = 32$, while a species with 4 wins, 30 ties, and 66 losses scores $[4 \times 3] + [30 \times 1] + [66 \times 0] = 42$, which gives a better ranking); W/T (proportion of wins over total number of interactions); L/T (proportion of losses over total number of interactions—rank 1 here is the smallest number, [i.e., a winning performance] and rank 11 is the largest number [i.e., a poor performance] and W/L (proportion of wins over losses). Two novel methods were also applied; they are described in recent literature (De Vries, 1998; Jameson *et al.*, 1999). Abbreviations of taxa are *Tegella armifera* (Ta), *Tegella aquilostris* (Tq), *Myrzoella plana* (Mp), *Caulorhamphus* sp. (Ca), *Microporella californica* (Mc), *Tegella arctica* (Tr). *Patinella* sp. (P), *Microporella* sp. (M), *Cribrilinea annulata* (Cn), *Porella alba* (Pa) and *Alcyonidium* sp. (A). The genus *Lichenopora* was revised by Gordon and Taylor (1997) and Recent species were reassigned to the genus *Patinella*. Cyclostome taxa are in shaded cells and printed in bold. Equals signs (=) signify that the taxa have equal ranking.

How do cyclostomes persist alongside superior space competitors?

Since the Mesozoic, cheilostomes have not only dramatically increased at various taxonomic levels (family, genus and species), but also maintained their historical competitive dominance over the cyclostomes (see Taylor, 1993; McKinney, 1995a; Jablonski *et al.*, 1997; McKinney *et al.*, 1998). Marine ecological studies of modern assemblages (such as those of Ireland and Antarctica in the present study) have revealed a variable but a distinct competitive edge of cheilostomes over cyclostomes (McKinney, 1992; Barnes and Dick, 2000). Despite the evolutionary and ecological increase of cheilostomes over the past 100 million years, cyclostomes have maintained global and local diversity (Lidgard *et al.*, 1993). The inevitable increased frequency of cheilostome-cyclostome meetings resulting from the proliferation of cheilostomes might be expected to bring about a progressive displacement of cyclostomes. This may have contributed to the decline in ecological success and species richness of cyclostomes from the end of the Cretaceous to the Recent (Lidgard *et al.*, 1993; McKinney *et al.*, 1998; Sepkoski *et al.*, 2000). The effect seems better explained, however, as merely adding to total bryozoan diversity rather than as displacement (Sepkoski *et al.*, 2000).

The comparative lack of effect on cyclostomes of the K-T boundary event (McKinney *et al.*, 1998) suggests that this clade has been very resilient in the face of major changes with time. Recruitment patterns revealed in the present

study show that cyclostomes are best positioned, not just amongst the bryozoans, but also throughout encrusting macrobiota, to exploit newly available habitats. Cyclostome recruits peaked high and early (Figs. 4 and 5) and were initially the dominant component developing subtidal assemblages at Lough Hyne (Fig. 6). Thus, on ephemeral substrata they gain advantage. In highly disturbed environments, such as the nearshore polar environment, cyclostomes should (and do), therefore, constitute a major portion of the lithophyllic biota (Barnes *et al.*, 1996; Barnes and Dick, 2000). The advantage of early colonization and establishment (Fig. 6) is maintained by a strategy that prevents overgrowth (Table 1). Thus persistence, rather than winning competitive encounters outright, is a feature of cyclostomes.

The evolutionary success (species richness) and ecological success (biomass) of the cyclostomes have been decoupled over geological time (McKinney *et al.*, 1998) and, during Recent times, in geographical space, as well. Localities where cyclostomes have their highest inter-clade performance levels are not linked with areas of greatest numerical abundance. Cyclostomes perform well against cheilostomes in Alaska and Ireland, but compete poorly on Antarctic rocks. Yet, of these localities, it is in Antarctica that they occupy most space (see Barnes and Dick, 2000; Barnes and Maughan, 2002). Cyclostomes are poorly represented at low latitudes (Taylor, 2001) and around some small island groups (Banta and Redden, 1990; Hayward and Winston, 1994). Between 45 °S and 75 °S, the relationship

between latitude and the ratio of extant cheilostome species to cyclostome species seems to be parabolic (Barnes and DeGrave, 2000). Cheilostomes constitute more than 70% of species (of the two clades) between 55 °S and 65 °S, and cyclostomes are nearly 50% at 50 °S and at 70 °S (Barnes and DeGrave, 2000). Causes of the differences in cheilostome and cyclostome species richness in the Southern Ocean may be linked to historical diversity centers and events in the Tertiary (*e.g.*, see Moyano, 1983; Winston, 1983) when Antarctica became isolated and ultimately polar (Lawver *et al.*, 1992).

How superior are cheilostomes to cyclostomes?

Determination of superiority in ecology is relatively straightforward, if only one aspect is considered. In fossil assemblages, an asymmetric performance relationship between cyclostomes and cheilostomes is clear-cut (McKinney, 1995a). The demonstration that Recent variability in performance is more than twice that in the fossil record (Barnes and Dick, 2000) casts doubt on the meaningfulness of mean performance scores for the two clades on large spatial or temporal scales. Only a weak relationship between site energy and performance is shown here (Fig. 7). In Ireland, the performance of cyclostomes against each functional group of cheilostomes increased slightly with currents of increasing energy, but this increase in performance was much less in the very high energy Antarctic waters. A further relationship, between local cyclostome performance and species richness (Fig. 8), suggests that further factors are yet to be determined. The variation in competitive performance with the particular index chosen to measure it (Table 1) complicates any overall assessment. Essentially, cyclostomes are fairly poor at gaining space from a competitor by physical contact. They are much more adept at avoiding being overgrown.

Depending upon the degree of crowding and competition, cheilostomes often initiate or increase their formation of brood chambers (reproductive activity) on contact with competitors (Barnes and Clarke, 1998). There is some evidence that fossil cyclostomes also initiated brood chamber construction when crowded by competitors. There is, indeed, even evidence that sexual reproductive activity may have been exclusively or nearly exclusively initiated by fossil cyclostomes coming into contact with competitors (McKinney and Taylor, 1997). When examining certain fossil cyclostomes, McKinney and Taylor (1997) found reproductive activity only in colonies that abutted other colonies. Certainly the peaks of cyclostome larvae appear just after an increase in cheilostome abundance at Lough Hyne (Fig. 5), though no distinct pattern is evident in the Antarctic data set (Fig. 6). Although cyclostomes appeared able to hold off most cheilostomes for the duration of the temperate and polar studies reported here, ultimately both

clades were easily overgrown by sponges and ascidians (Maughan and Barnes, 2000), as has been found elsewhere (Russ, 1982; Sebens, 1986). At Lough Hyne and Signy Island, more than 90% of spatial competitive encounters by cyclostomes were against cheilostomes. The cyclostome survival strategy is to hold off their most common competitor, cheilostomes, until larvae can be produced; and this may be an effective plan. Whether the high proportion of stalemates between representatives of the two clades is permanent may be irrelevant, for both clades may then be overgrown by other superior space competitors.

Comparable densities of recruits (Figs. 4 and 5) indicate that the reproductive output of the two clades is similar at the two very different study sites. However, when recruitment and space occupation at the same locality are considered, cheilostomes must grow considerably faster. At Signy Island, the absolute number of cheilostome species recruiting was considerably greater than the number of cyclostomes, with the mean number of species recruiting per unit time oscillating around 50%. Furthermore, in the two study assemblages, as established for the fossil record (McKinney *et al.*, 1998), taxonomic richness patterns did not reflect ecological dominance. In summary, the extent of superiority of cheilostomes is highly variable; it depends both on attribute (reproduction, growth, or spatial competition) and, as shown by Table 1, on how superiority is measured.

What makes cheilostomes superior to cyclostomes—better by design?

Evolution of cheilostome and cyclostome skeletal structure has followed similar and often convergent paths. The sequence of origin of structural novelties was similar between the two clades, but the timing and speed of acquisition (Fig. 9) was not (Jablonski *et al.*, 1997). Because most structural novelties of cyclostomes originated more than 50 million years earlier than those of cheilostomes, the ecological context of their design innovations are different: that is, cyclostome novelties evolved during a period of relatively low and stable familial and generic diversity, whereas those of cheilostomes appeared during a phase of high and rapid increase of diversity (Fig. 2). The design of cheilostomes made them certain to be superior competitors to cyclostomes, although chance has probably played a major role in survival of many groups of organisms. Cheilostomes possess many superior attributes focused at the colony margin, where (1) zooidal skeletons and feeding structures are full-sized because of rapid ontogenetic development; (2) labile morphogenetic responses (such as raising growing edges, frontal budding, and stolon production) are possible; and (3) excurrents are produced (McKinney, 1992; 1993; 1995a, b). The latter discovery, along with others from studies of fluid dynamics, has important ramifications for inter-clade competition. Cyclostome incurrents emanate

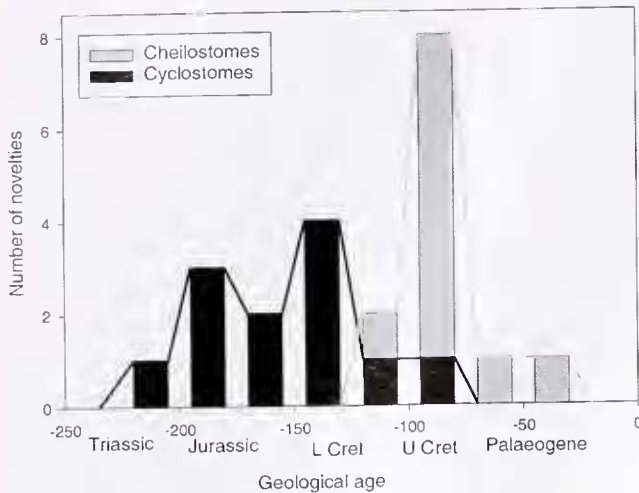


Figure 9. Evolution of morphological novelties in the cyclostome and cheilostome clades plotted against geological age. Figure adapted from Jablonski *et al.*, (1997).

from the periphery; therefore, in competition with a cheilostome neighbor, cyclostome incurrents are potentially the excurrents of cheilostomes. Cheilostome incurrents, in contrast, are drawn down from the water above a colony and are thus separated from the excurrents of a neighbor. Fisher (1989) has suggested that an element of chemical warfare exists, whereby feces can be passed from one competitor into the feeding current of its neighbor (though this study featured only cheilostomes). The combination of these features, combined with higher growth rates, larger colonies, and feeding structure novelties—and possibly the acquisition of non-planktotrophic (lecithotrophic) larvae, have made possible the great radiation of the cheilostomes since the mid-Cretaceous period (Taylor, 1988; Lidgard *et al.*, 1993). Despite the generalities of inter-clade differences (discussed above), the design and structure of bryozoans are characterized by significant intra-clade variability and inter-clade overlap. The cheilostome clade incorporates a huge range of colony forms, including spot, runner (stolon), membranous sheets, bilaminar foliaceous sheets, and a variety of erect forms of flexible or rigid structure. Some of these forms strongly resemble those of certain cyclostomes. Spot colonies, such as those of the cheilostome *Cribrilina* (Bishop, 1989), are similar in shape, structure, and even performance in spatial competition to the cyclostome *Patinella* (Table 1). Although cheilostomes can generally be considered to have a superior design, the range of colony form effectively incorporates most cyclostome structures.

Why have the cyclostomes declined ecologically over the last 100 million years?

Despite the revival of ecological dominance for at least 5 million years after the K-T extinctions (Fig. 3, and see

McKinney *et al.*, 1998), cyclostomes have, for the last 90 million years, constituted only a minor proportion of bryozoan taxa and of skeletal mass, aside from the early Cenozoic excursion. Although cyclostomes have maintained family diversity levels, neither generic richness nor species richness has recovered from the end-Cretaceous crashes.

The lower rate (post K-T) of origination of cyclostome genera has mostly accounted for their decline relative to cheilostomes (McKinney and Taylor, 2001). But erect, rather than encrusting, species are mainly responsible for this pattern (P. D. Taylor, Natural History Museum, London, unpub. data), which highlights a major problem with inter-clade comparisons based on existing knowledge. Although most evidence and discussion concerns encrusting species, as in this study, some changes may have little to do with this colony form. Interpretation of comparative historical records of a clade is difficult for many reasons, including increase of species diversity along nonlinear paths over macro-evolutionary time (Fig. 2; Sepkoski, 1979, 1991) and differential rates of evolution between clades. Specific diversification of clades seems to be controlled by a number of factors, such as the resolution of resource division (Bambach, 1983, 1985), presence and identity of other competing clades (Kitchell and Carr, 1985), and clade-specific speciation and extinction rates (Sepkoski, 1996). Cyclostome displacement may have largely occurred through increased meetings with typically superior competitors (cheilostomes) from end-Cretaceous to Recent time (Lidgard *et al.*, 1993; McKinney, 1995a; Sepkoski *et al.*, 2000). Such a displacement may have been merely geographic. As with species niche shifts, cyclostome species and abundance centers may have shifted to occupation of a "realized niche" at higher latitudes. Although niche shifts have been much discussed at the species or genus level, the same process could theoretically occur at higher taxonomic levels.

Recent assessments of the consistently asymmetric performance in interference competition between the two clades, carried out in living and fossil assemblages (McKinney, 1992 and 1995a, respectively), were important pieces of evidence supporting competition as an explanation for absolute clade displacement. Although this conclusion may be true for the types of environments ideal for fossilization (shallow, warm, low-energy seas), it is clearly not applicable to all geographic regions (Barnes and Dick, 2000). In high-energy environments, performance and space occupation by cyclostomes may differ considerably. Thus, rather than necessarily having diversity and abundance depressed by cheilostome competition, cyclostomes could have undergone a clade niche shift to higher energy conditions—a shift that may be unrepresented in the fossil record because of differences in the likelihood of environmental preservation. Whether competition has been entirely responsible for such a shift is debatable. The competitive performance of cyclostomes increases with increased en-

ergy conditions (Fig. 7), and their increased occupation of space in high-energy conditions provides some supporting evidence for a shift along an energy gradient. In contrast, other data from the northern Adriatic Sea shows decreasing cyclostome richness and diversity with increasing site energy (F. K. McKinney, Appalachian State University, North Carolina, unpubl. data).

Conclusions

Despite fluid dynamic, ultrastructural, and morphogenetic evidence of cheilostome design superiority, cyclostomes persist through differential recruitment strategy, rapid colonization, and maintenance of space. Some of the multiple methods of survival have only recently begun to be recognized by biologists. Rather than being a rare or temporary event, tied outcomes may be a regular outcome in competition between certain taxa (Stebbing, 1973; Russ, 1982; Sebens, 1986; McKinney, 1992; Barnes and Dick, 2000), and may represent a temporally stable state (Tanaka and Nandakumar, 1994). Only with understanding of these concepts is cyclostome strategy becoming apparent. Therefore, cheilostome expansion may have indeed added to bryozoan diversity, and cyclostomes may have undergone some geographical displacement possibly mediated by inter-clade competition. Ecological and evolutionary success is clearly decoupled in cyclostomes at global and local levels. Domination in early community development or after disturbance is possible at varying geographical and temporal scales despite the prolific expansion of a competitively superior and co-occurring elade (cheilostomes).

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